THE SIR WILLIAM MACLEAY MEMORIAL LECTURE 1980

Cambrian Animals: their Ancestors and Descendants

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[Delivered 10 September 1980]

Synopsis

In the largely soft-bodied, Cambrian, Burgess Shale fauna, species intermediate between major taxa are unknown, wide morphological gaps separate species of arthropods and worms, and there is a high proportion of animals which cannot be placed in any recognized group. Morphological discontinuities also separate earliest known kinds of trilobites, brachiopods and echinoderms, and species of the latter group occur in widely separated geographical areas. New discoveries extend back in time the ranges of major taxa, so that the Cambrian pattern of evolution shows many discrete, parallel lines of descent, which may reflect less strong competition during the initial occupation of marine environments. In the Ordovician period many groups having hard parts show spectacular adaptive radiation patterns, concomitant were extinctions of many of the strange animals of the Cambrian, and in succeeding periods Recent phyla become dominant. The complex pattern of Phanerozoic evolution reflects varying rates, extinctions, and the influence of geography on isolation as well as dispersal. The Precambrian pattern may have been equally complex because of similar factors. Metazoan animals may have arisen more than once, first soft-bodied, later secreting hard parts, and the arthropod, brachiopod, echinoderm or other grade of organization may have arisen independently in separate lines of descent.

Sir William Macleay studied living animals from the land and the sea, but he was aware of palaeontological work, for his collections included Palaeozoic fossils. The theme of this Memorial Lecture is what the oldest fossils reveal about the early evolution of the marine faunas that engaged Macleay's attentions. At most fossiliferous localities in Cambrian rocks only the hard parts of invertebrate marine animals are preserved. These parts may be dissociated, fragmentary, or altered in composition or shape from their original condition. Relatively rarely the hard parts are well-preserved, and still more rare are localities at which traces of soft parts have been found. It is from such remains that the palaeontologist tries to reconstruct the once-living animal, suggest its activities, and surmise how it may have been related to older and younger forms. The rare fossils which have soft parts preserved assume major importance in such work. However imperfect their preservation, and irregular their occurrence in time and space, fossils reveal kinds of animals that lived in the past, and thus the course of evolution. This unique evidence has to be integrated with that from biology if we are to understand evolutionary patterns. In recent years there has been a renewed interest in such patterns and in relationships within and between major groups (e.g. Hallam, 1977; House, 1979), and a vigorous controversy about the application of Hennig's methods in palaeontology (e.g. Campbell, 1975; Cracraft and Eldredge, 1979). Diagrams portraying relationships between major groups of animals have long been argued (e.g. Kerkut, 1960, pp. 101-111; Valentine, figs. 1, 2, pp. 29, 38, *in* Hallam, 1977). They show a single type of animal at the base, and an upward, ever-increasing number of branches. Whether or not such diagrams imply that metazoans arose from a single stock is not explicit, but if they are intended to do so, it follows that metazoans arose from a single interbreeding population, a species that occupied a particular geographical area at a particular time in the past. However, Cloud (1968) suggested that the metazoan grade of organization may have arisen more than once, implying that 'stem metazoans' arose more than once, in different areas at different times. New palaeontological discoveries are extending back in time the earliest occurrences of kinds of animals, but have not revealed animals intermediate in structure between major groups. It is assumed by many authors that animals having basic structures in common, such as jointed limbs (arthropods), or a particular microstructure of the hard parts (echinoderms), had a common ancestor. Palaeontology has not so far provided firm evidence for or against this assumption, but does not appear to exclude the possibility that higher grades of metazoan organization, even of animals which secreted hard parts, may have arisen independently in different geographical areas.

In any consideration of marine faunas of the Cambrian period, that of the Burgess Shale must loom large, because of the exquisite preservation of some 150 species of animals, two thirds of which lacked hard parts. It gives us a highly

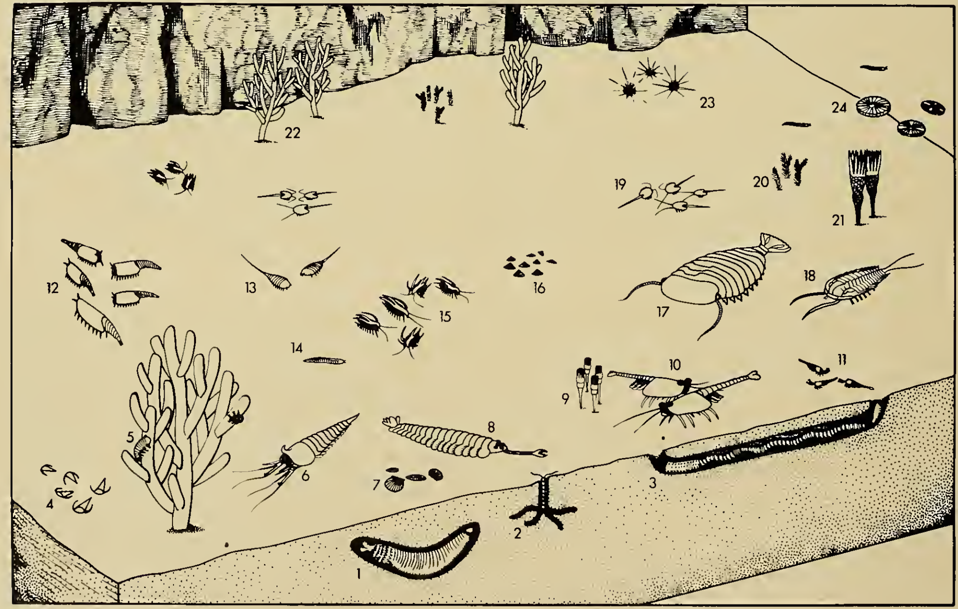

Fig. 1. Diagrammatic representation of some of the species of the Burgess Shale fauna which lived above, on and in the muddy sediments deposited at the foot of a submarine cliff (in background) considered to have been over 100 m high. Animals shown have been numbered from left to right in successive rows across the drawing, beginning with the vertical section in the foreground: branching and globular sponges (*Vauxia*, 22; *Choia*, 23; *Pirania*, 20), the articulate brachiopod *Nisusia* (7), the monoplacophoran mollusc *Scenella* (16), *Hyolithus* (4), the coelenterate *Peytoia* (24), two priapulid (*Ottoia*, 1: *Louisella*, 3) and one annelid (*Burgessochaeta*, 2) worm, a variety of arthropods (the trilobite *Olenoides*, 18; the non-trilobites *Sidneyia*, 17; *Leanchoilia*, 6; *Marrella*, 15; *Canadaspis*, 12; *Molaria*, 13; *Burgessia*, 19; *Yohoia*, 11, *Waptia*, 10; and *Aysheaia*, 5, crawling on the sponge *Vauxia*, 22), the echinoderm *Echmatocrinus* (21), the chordate *Pikaia* (14). In addition are shown two animals of uncertain affinities, *Opabinia* (8) and *Dinomischus* (9). The animals are drawn to show approximate relative size. This diagram is a variant on an earlier one by Conway Morris and Whittington (1979), drawn from my sketches by Adele Prouse.

significant glimpse of early Middle Cambrian metazoans (Whittington, 1980 and references) that appear to have lived on, in and above the muddy sea bottom at some 100 m depth (Fig. 1). Over 50,000 specimens were collected by Charles D. Walcott from this unique locality in British Columbia, Canada. About one-third are of the two arthropods, *Marrella* and *Canadaspis*, and next most abundant are the arthropod *Burgessia*, the priapulid, burrowing worm *Ottoia*, and certain of the sponges. Less abundant are the arthropods *Yohoia, Waptia, Sidneyia* and *Molaria*, while others such as *Leanchoilia* and *Aysheaia* are rare. Not shown in Fig. 1 is *Anomalocaris*, an animal which may have reached a length of 1 m, but only the large detached limbs are known. The arthropods, including trilobites, dominated the preserved fauna in numbers and kinds, and were particle feeders, predators and scavengers, walking on the bottom, digging into it, and drifting and swimming above it. Coelenterates, inarticulate and articulate brachiopods, and annelid worms were not abundant, the cap-shaped shells of the monoplacophoran, and hyolithids, being commoner. A few species of chordates, hemichordates, and echinoderms are known, each rare and strikingly different from others in the group. Second in variety of kinds to the arthropods are the sponges, and third is an assemblage of miscellaneous animals which cannot be placed in any recognized group. Fig. 1 shows two examples of the latter: *Opabinia*, a worm-like animal which had a flexible frontal process for food-gathering, and the sessile *Dinomischus,* a cup fringed with plates, anchored by a long stem.

This fauna was seemingly not that of an isolated backwater, but inhabited muds at the foot of a submarine cliff, facing the ocean, on the present western side of the North American continent. This site was open to migration, but how widespread the fauna may have been is unknown. In the shallow waters around other continents of Cambrian times there may have been equally varied and different faunas — there certainly were different faunas of animals with hard parts, and perhaps in them soft-bodied animals were twice as varied in kinds. The significance of the Burgess Shale fauna is that it opens a new perspective on Cambrian animals, for among its characteristics are:

1) the wide morphological gaps between kinds of animals in groups such as worms, echinoderms and arthropods. In the latter, for example, there are rarely two related species of a genus, most genera are monospecific and separated from each other at a family, or higher taxonomic level, and most have no known descendants;

2) an absence of animals showing structures intermediate between those of any two phyla (Conway Morris, quoted by Valentine *in* Hallam, 1977, p. 32);

3) particular species which show characters typical of major later groups, such as the crustacean *Canadaspis*, the crinoid-like *Echmatocrinus, Pikaia* with its chordate-appearing structures, and such animals as the onychophoran-like *Aysheaia*, the kind from which tardigrades, myriapods and insects may have been derived;

4) a high proportion (19 per cent) of the genera are animals that cannot be placed in any Recent higher taxon, a few such animals are known from soft-bodied faunas of younger Palaeozoic rocks but none so far as I am aware from rocks of subsequent eras.

The only Precambrian metazoans known are the late Precambrian Ediacara faunas (Glaessner, 1979), widely distributed, three-quarters of them coelenterates (mainly medusae), and a few genera of supposed annelids and arthropods, together with the enigmatic *Tribrachidium*. This assemblage of soft-bodied organisms, preserved in unusual circumstances in shallow-water environments, offers little clue to the ancestry of Cambrian animals. Precambrian sponges and archaeocyathids are unknown, as are skeleton-forming protistans. If the Burgess Shale fauna is assumed to be typical of mid-Cambrian marine faunas, then evidently a great diversification had taken place earlier. Presumably there was abundant food and space in the varied marine environments which were being occupied initially by these new animals, and competition was less severe than in succeeding periods. In these circumstances diverse combinations of characters may have been possible, as new ways of sensing the surroundings, of obtaining food, of moving about, of forming hard parts, and of behaviour (e.g. predation and scavenging) were being evolved. Thus may have arisen strange animals, the remains of some of which we see in the Burgess Shale, and which do not fit into our classification. The diverse arthropods may have arisen from different ancestors, not diverged from a single ancestral stem, by sclerotization of the exoskeleton. In the earliest Cambrian are three very different kind of trilobites, the eodiscoids, olenelloids, and ptychoparioids. They may not have had a common ancestry, but have arisen from discrete, soft-bodied, segmented metazoans. Having acquired the ability to mineralize the exoskeleton, and so to appear as fossils, they each radiated from the stem type during the Cambrian period. A similar suggestion as to brachiopod ancestry has recently been made by Wright (*in* House, 1979), who proposes that the heterogeneous groups of the early Cambrian arose independently from different lophophorates, worm-like animals having a crescentic lophophore. A further possible example is afforded by the several strange echinoderms, each localized in time and space, of the western United States (Sprinkle, 1976), the unique early Cambrian lepidocystids of the eastern United States (Sprinkle, 1973), and the enigmatic remains from Queensland (Whitehouse, 1941). Each may have evolved independently in a different geographical area, preserved when it acquired the ability to secrete the characteristic endoskeleton. The influence of geography on Cambrian evolution in the marine realm was undoubtedly strong, but difficult to assess. Fig. 2 is a Middle Cambrian palaeogeography, which in common with other such maps shows a large Gondwanaland continent and an uncertain number of other, smaller land areas. Shallow seas, in which Cambrian rocks were deposited, surrounded the land masses, separated one from another by oceans of uncertain width and depth. These oceans, and the current patterns would have acted as filters, partial barriers to migration between shallow seas. Evolution may thus have proceeded independently in different areas at particular times, and the distribution of kinds of trilobites and echinoderms in the Lower and Early Middle Cambrian suggests that it may have. The Cambrian period may have lasted 70 or more million years, and the Ediacara fauna is thought to have lived 80 or 100 million years before the beginning of the Cambrian. During these immense lengths of time continental masses may have moved great distances relative to one another. How such relative movements may have aided geographical isolation or dispersal is unknown, and knowledge of the distribution in time and space of Cambrian faunas is inadequately known. Thus the geographical factor in the early evolution of metazoans is impossible to assess at present, but should not be discounted.

During the Cambrian period particular groups of animals appear to have radiated into many related species, genera and families, and become widespread. The Archaeocyatha of the Lower Cambrian, and the major groups of trilobites, especially the ptychoparioids, are conspicuous examples. Other groups are present but markedly limited in kinds, such as the articulate brachiopods and diverse but rare echinoderms. Molluscs (Runnegar, 1980) are diverse in kinds but not common fossils, and many are of small size (Runnegar and Jell, 1974). The Burgess Shale reveals something of the variety of arthropods and worms that had evolved, as well as miscellaneous animals, but it would have been difficult for a contemporary observer to have picked out the crustacean *Canadaspis*, the chordate *Pikaia*, or *Aysheaia* as fore-runners of groups that would later become so important in so wide a variety of environments. In the latest Cambrian and succeeding Ordovician period the variety of shelled animals in

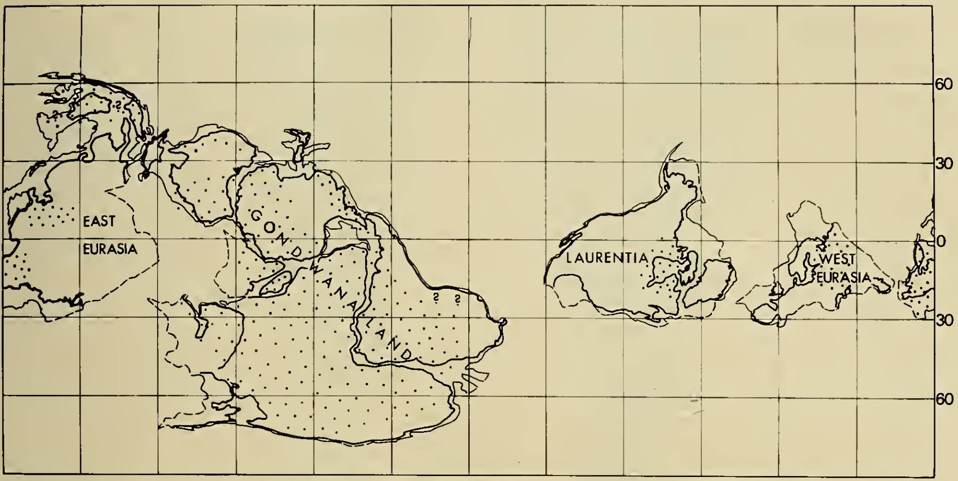

Fig. 2. Middle Cambrian palaeogeography, based upon Smith, Hurley and Briden (in press), cylindrical equidistant projection. Each continental block is delineated by a thin continuous or dashed line at the present 1000 m submarine contour, inside which is a heavier line showing the present coastline as an aid to recognition. The division between East and West Eurasia is at the Urals, and West Eurasia lies north of the present Alpine chain. There is great uncertainty about the position of the four continental masses, and the gaps between them may have been greater or less than shown. Stipple shows areas where Cambrian rocks are unknown, and which may have been land (after Palmer, *in* Hallam, 1973; 1979). The remainder of each continental block was probably covered by sea.

marine communities increased, with major radiations of articulate brachiopods, bryozoans, pelecypods, gastropods, cephalopods, tabulate and rugose corals, trilobites and classes of echinoderms. Many of these groups are preserved for the first time, and in most cases their Cambrian ancestors are problematical (various authors *in* House, 1979). Each of these radiations was a typical diversification giving related species, families and genera, and does not show the morphological gaps between species so characteristic of many Cambrian groups. It was a time of much stronger competition for food and space, of radiation of groups which happened to be best adapted, following the elimination of those that were not. In the Ordovician and younger periods (Hallam, 1973), sufficient is known to reveal in some detail faunal provinces and the importance of geographical factors in evolution.

From the foregoing I select the following points:

a) Geographical isolation as well as dispersal, affected the evolution of early metazoans, so that animals may have arisen that were similar in organization but independent in origin. Such animals may have acquired the ability to secrete hard parts in similar ways, at the same time, or at different times, in these independent lines of descent. Thus the earliest trilobites, brachiopods or echinoderms may not have had a common ancestry, but rather be animals of similar organization which had separate origins.

b) If the Burgess Shale fauna was characteristic of world faunas, then soft-bodied animals may have been far more numerous and varied than animals with mineralized skeletons. Characteristic of these soft-bodied faunas may have been the morphological discontinuities between kinds, for example of arthropods and worms; they may not have been groups of closely related species and genera. During the Cambrian period certain groups which had hard parts, such as molluscans and articulate brachiopods, remained restricted in numbers and kinds, whereas trilobites and archaeocyathids, which also had hard parts, evolved in a typical radiating manner and were widely distributed. An exceptionally high proportion of kinds of soft-bodied animals may have been so strange in organization that they could not have been placed in our presently-recognized higher taxa, even at phylum level. Because the Cambrian was the time when marine environments were first being occupied by animals varied in morphology and habit, competition may have been less severe than in subsequent periods. In these circumstances, for example, widely different animals with jointed legs may have evolved, and also animals having new combinations of structures and ways of living. Evolution in the Cambrian seems to have had a different character from that of later periods.

c) Neither in the Burgess Shale nor at other localities have been found animals which are intermediate between phyla. New discoveries, such as the probable chordate *Pikaia,* what appears to be a Middle Cambrian rugose coral (Jell and Jell, 1976), or an early Cambrian pelecypod (Jell, 1980), take the range of known kinds of animals farther back in time.

d) Late in the Cambrian period, and soon thereafter, came the major radiations of groups with hard parts. During the Palaeozoic strange arthropods and animals of unknown affinities (leaving aside those having problematic hard parts, such as conodonts) became progressively rarer and do not seem to be known after this era. Thus many of the strange animals of the Cambrian were eliminated as others radiated to occupy a wide variety of environments. Pre-adaptation and selection acted as a filter, extinguishing many lines and leaving those that have come to dominate later Palaeozoic to Recent times. A diagrammatic representation of such an evolutionary pattern (Fig. 3) shows in the early Palaeozoic many lines of descent, parallel and of varying duration. On the left side are lines, most of which extend from the Precambrian or early Palaeozoic to the present, and represent the largely unknown geological history of the modern soft-bodied marine faunas. The Ediacara fossils imply that some at least originated early. Area A suggests that a group of animals with hard parts may appear abruptly, descended from soft-bodied ancestors which may have had a long history; an example may be the Mesozoic hexacorals (Oliver, 1980). On the right of Fig. 3 are parallel lines which represent the plethora of soft-bodied animals, some arthropods and others of unknown affinities, upon which the Burgess Shale opens a partial window. Most of these may have been eliminated in the early Palaeozoic, few persisting longer. Typical histories of major groups of animals with hard parts are shown by the shaded areas. Area B might represent the post-Cambrian expansions of gastropods, pelecypods or cephalopods, or of echinoderms, from somewhat uncertain Cambrian ancestors and after elimination of strange early types. The post-Palaeozoic renewals are also shown. Area C represents trilobites, a Cambrian radiation from diverse early lines, a new burst of evolution in the Ordovician followed by decline and extinction. Area D could represent the mid-Palaeozoic conquest of the land by myriapods and insects, perhaps to be traced back to Cambrian marine animals of *Aysheaia* type; it could represent vertebrate history. The isolated Lower Cambrian Archaeocyatha are suggested in area E. The diagram does not indicate the existence of forms intermediate between phyla, because none is known.

The major taxa that we use are based largely on Recent faunas, and are relatively easily extended back through the Cainozoic and Mesozoic into the middle Palaeozoic. They are retrospective, subdivisions of the living world, made after 800 million years or more evolution of metazoans. What animals should, or should not, be placed in these phyla and classes becomes more a matter of debate as one goes back into the Cambrian, and what we know of Precambrian metazoa is also difficult to fit into Recent groupings. The strangeness of Cambrian metazoans, the large morphological

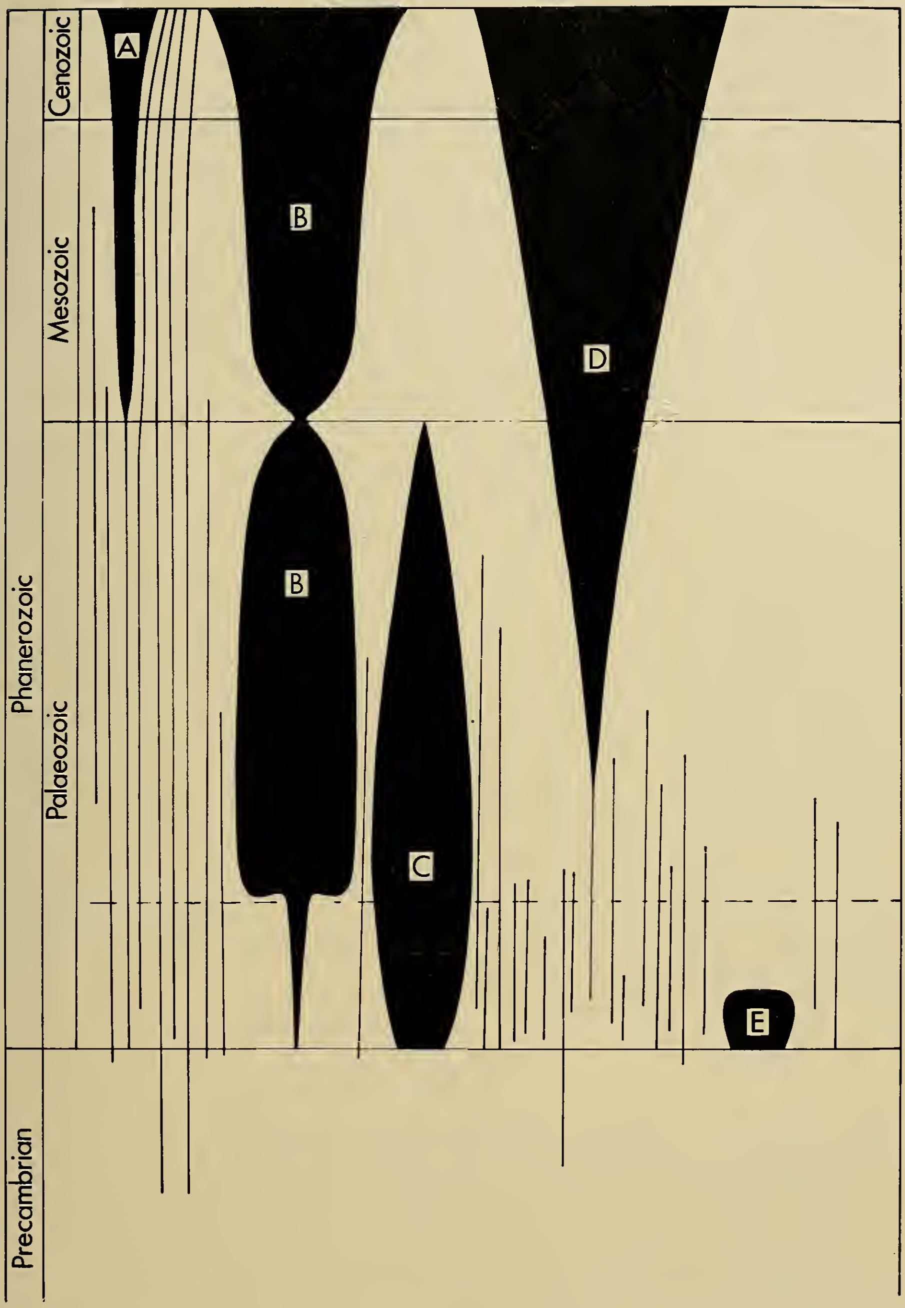

Fig. 3. Diagram expressing the pattern of Phanerozoic evolution in metazoan animals suggested by palaeontology. Thin continuous lines represent known and unknown groups without hard parts, black areas groups with hard parts. Width of black areas suggests increase or decrease of numbers of kinds in time. No two lines are shown joining downwards because animals intermediate between major groups are not known. Vertical axis is time, horizontal line is omitted at base of diagram because the Precambrian was approximately seven times as long as the Phanerozoic. Horizontal dashed line indicates boundary between Cambrian and Ordovician periods.

gaps that characteristically separate the forms, may be a pointer to how evolution proceeded. I suggest that in the late Precambrian and Cambrian when the evolution of plants had provided ample food in a wide variety of environments, metazoans evolved independently around the margins of scattered continents. Migrations and increases in numbers and kinds led gradually to occupation of available environments, so that competition intensified during the Cambrian. The Burgess Shale, by chance of preservation, shows us a selection of these strange creatures, some of which appear to be the ancestors of groups which subsequently radiated and became the major taxa of the living world. Large numbers of these animals may have been relatively short-lived, successions of populations which lasted only a few tens of millions of years, and have little place in our records. This filtering process in the latest Cambrian and succeeding period led, through combinations of circumstances which are still obscure, to the emergence of the major groups. The pattern is thus one of limited but persistent beginnings, followed by the adaptive radiation that established the group, a pattern repeated, for example, by mammals in the Mesozoic and Cainozoic. In outlining this pattern it is customary to show a single origin. However, palaeontological evidence (Fig. 3) begins after an unknown history of metazoan animals, of uncertain length, in a world so far hidden even in outline. The pattern of Phanerozoic evolution reveals that the rate varied, from place to place as well as in time, and that extinctions as well as radiations and dispersals played their part. The preceding pattern may have been equally complex, resulting from independent origins, varying rates, and extinctions. In his preface Kerkut (1960) writes that he will 'present evidence for the point of view that there are many discrete groups of animals and that we do not know how they have evolved nor how they are interrelated. It is possible that they might have evolved quite independently from discrete and separate sources'. In the early Phanerozoic there are many discrete lines of descent, the relationships between which are matters of speculation. Whether or not they had a single origin is an open question, and evolutionary patterns in the Precambrian may have been as complex as those of the Phanerozoic.

I am greatly honoured to have been invited to give this lecture, and thank Professor G. M. Philip, University of Sydney, for making my visit possible, and enabling me to discuss these ideas with a wide circle of Australian colleagues. In England I have received helpful comments on the manuscript from Drs D. W. T. Crompton, S. Conway Morris, and R. A. Fortey.

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